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# Navigating the complexity of ecological stability

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## 1   **Abstract**

2   Human actions challenge nature in many ways. Ecological responses are ineluctably complex,  
3   demanding measures that describe them succinctly. Collectively, these measures encapsulate the  
4   overall “stability” of the system. Many international bodies, including the Intergovernmental  
5   Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), broadly aspire to  
6   maintain or enhance ecological stability. Such bodies frequently use terms pertaining to stability  
7   that lack clear definition. Consequently, we cannot measure them and so they disconnect from a  
8   large body of theoretical and empirical understanding. We assess the scientific and policy literature  
9   and show that this disconnect is one consequence of an inconsistent and one-dimensional approach  
10   that ecologists have taken to both disturbances and stability. This has led to confused  
11   communication of the nature of stability and the level of our insight into it. Disturbances and  
12   stability are multidimensional. Our understanding of them is not. We have a remarkably poor  
13   understanding of the impacts on stability of the characteristics that define many, perhaps all, of the  
14   most important elements of global change. We provide recommendations for theoreticians,  
15   empiricists and policymakers on how to better integrate the multidimensional nature of ecological  
16   stability into their research, policies and actions.

## 17 **Introduction**

18       Species live in a web of prey and other resources, mutualists, competitors, predators, diseases,  
 19 and other enemies (Montoya *et al.* 2006; Bascompte 2009; McCann & Rooney 2009; Kéfi *et al.*  
 20 2012; Tilman *et al.* 2012). All encounter a profusion of diverse perturbations in their environment,  
 21 both natural and human-induced, that vary in their spatial extents, periods, durations, frequencies  
 22 and intensities (Tylianakis *et al.* 2008; Miller *et al.* 2011; Pincebourde *et al.* 2012; MacDougall *et*  
 23 *al.* 2013). These multifaceted disturbances precipitate a range of responses that can alter the many  
 24 components of ecological stability and the relationships among them (Donohue *et al.* 2013). This  
 25 complexity necessitates a multidimensional approach to the measurement of stability. We examine  
 26 the extent of our understanding of the multidimensional nature of both disturbances and stability.  
 27 We find that it is highly restricted. Consequently, our ability to maintain the overall stability of  
 28 ecosystems for different management and policy goals is limited. If ecology is to support and  
 29 inform robust and successful policy, we must rectify this.

30       At least three scientific communities use terms that map onto various dimensions of  
 31 ecological stability. Theoreticians, for example, have developed an extensive literature on whether  
 32 the population dynamics of multi-species systems will be asymptotically stable in the strict  
 33 mathematical sense (May 1972; Thébault & Fontaine 2010; Allesina & Tang 2012; Rohr *et al.*  
 34 2014), or resilient, in the sense of a fast return to equilibrium following a small disturbance (Pimm  
 35 & Lawton 1977; Okuyama & Holland 2008; Suweis *et al.* 2013), and other well-defined measures  
 36 (see, for example, Pimm 1984; McCann 2000; Ives & Carpenter 2007). Empiricists observe and  
 37 manipulate natural systems or variously perturb experimental ones to measure ecological responses  
 38 in constant or naturally changing environments (Tilman *et al.* 2006; O’Gorman & Emmerson 2009;  
 39 Grman *et al.* 2010; Carpenter *et al.* 2011; de Mazancourt *et al.* 2013; O’Connor & Donohue 2013;  
 40 Hautier *et al.* 2014). Finally, many international bodies concerned with environmental conservation  
 41 aspire to maintain, protect, and sustain nature and avoid altering and degrading it, all for informing

42 decision makers and aspiring to enrich people's lives and well-being (Mace 2014; Díaz *et al.* 2015;  
43 Lu *et al.* 2015).

44 We explore whether the associated three scientific literatures engage each other in using the  
45 same terms and employ the same meanings for them when they do. Generally, they do not. We  
46 must remedy this. International bodies need terms that are simple and flexible, but surely not to the  
47 point of being meaningless. Theory cannot advance usefully in isolation from tests of it (Scheiner  
48 2013), and theory, experiment, and observation must sensibly inform decision makers at all levels.  
49 Most importantly, the multidimensional complexity of natural responses to environmental change  
50 needs to be recognised by all communities, both separately and collectively.

51 We suggest solutions to help achieve these goals. For theoreticians, we provide suggestions  
52 on where to focus future research to incorporate the sort of complexities commonly encountered in  
53 natural systems. Empiricists will find useful our summary of the methodologies developed so far to  
54 study the different facets of ecological stability and our recommendations for better assessing  
55 stability in collaboration with theoreticians and policymakers. Finally, we provide suggestions for  
56 environmental policymakers on how to develop and frame objectives and targets that are not only  
57 relevant for policy but at the same time facilitate much closer links with the supporting, and  
58 evolving, science.

59

## 60 **The multifaceted nature of disturbances and ecological responses**

61 Disturbances are changes in the biotic or abiotic environment that alter the structure and  
62 dynamics of ecosystems. Although they occur at a variety of scales and vary in their direct and  
63 indirect effects on species, all disturbances comprise four key properties; their magnitude, their  
64 duration, their frequency and how they change over space and time (Sousa 1984; Benedetti-Cecchi  
65 2003; García Molinos & Donohue 2011; Pincebourde *et al.* 2012; Tamburello *et al.* 2013). The  
66 magnitude of a disturbance is defined by how much the aspect of environmental change departs  
67 from its undisturbed state (*i.e.* “*a measure of the strength of the disturbing force*”; Sousa 1984). A

68 minor storm versus a once in 100-year hurricane is an example of disturbances that vary in  
 69 magnitude. Their duration refers to a continuum with instantaneous pulses — short, sharp  
 70 shocks — and sustained presses — constant, long-term change — at the ends of the spectrum (Fig.  
 71 1a). A discrete pollution event, such as a chemical spill, is a pulse, and the extinction of a species  
 72 from an ecosystem is a press. Theoreticians focus primarily on one of these two extremes of the  
 73 duration gradient (Ives & Carpenter 2007). Empiricists sometimes refer to these extremes as acute  
 74 and chronic disturbances, respectively.

75 Natural disturbance regimes are clearly more complicated than this. Changes in the  
 76 magnitude, duration and frequency of disturbances over time or in space can combine to give  
 77 disturbances directionality (Fig. 1b). Directionality measures the trajectory of change, which can be  
 78 highly dynamic and variable in terms of its mean and variance. Both can elicit distinct ecological  
 79 responses (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; García Molinos & Donohue 2010,  
 80 2011; Pincebourde *et al.* 2012; Mrowicki *et al.* 2016). Many of the most globally important  
 81 disturbances in nature are of this kind (Fig. 1c). Therefore, while a focus on pure pulse or press  
 82 disturbances provides some important insight into mechanisms that can underpin biological  
 83 responses to disturbances, the relevance of this to predicting responses to real disturbances in the  
 84 natural world may be limited.

85 While the multifaceted nature of disturbances creates a problem for assessing, understanding,  
 86 and predicting how ecological systems respond (García Molinos & Donohue, 2010; Mrowicki *et al.*  
 87 2016), the ecological responses themselves are also complex. Ecological stability is a  
 88 multidimensional concept that tries to capture the different aspects of the dynamics of the system  
 89 and its response to perturbations. Pimm (1984) reviewed five components of ecological stability  
 90 that are in common use. *Asymptotic stability* is a binary measure describing whether a system  
 91 returns asymptotically to its equilibrium following small disturbances away from it. One measures  
 92 *variability*, the inverse of stability, as the coefficient of variation of a variable over time or across  
 93 space. *Persistence* is the length of time a system maintains the same state before it changes in some

94 defined way. It is often used as a measure of the susceptibility of systems to invasion by new  
 95 species or the loss of native species. *Resistance* is a dimensionless ratio of some system variable  
 96 measured after, compared to before, some perturbation. *Resilience* is the rate at which a system  
 97 returns to its equilibrium, often measured as its reciprocal, the return time for the disturbance to  
 98 decay to some specific fraction of its initial value. Systems with shorter (faster) return times are  
 99 more resilient than those that recover more slowly. Holling (1973) introduced another definition of  
 100 resilience that is currently in common use, particularly in policy fora (Walker *et al.* 2004; Hodgson  
 101 *et al.* 2015). It “*is a measure of the persistence of systems and of their ability to absorb change and*  
 102 *disturbance and still maintain the same relationships between populations or state variables.*” This  
 103 definition is multidimensional. It integrates persistence, resistance and the existence of local  
 104 asymptotic stability at multiple equilibria. It has come to mean whether or not a system returns to  
 105 its former equilibrium following disturbance or moves to another one. This idea may be expanded  
 106 further to compare systems in terms of what range of disturbances a system can withstand before  
 107 being shifted to a new equilibrium (Ives & Carpenter 2007). If there is a limit beyond which a  
 108 system cannot return directly to its former state, this is termed a *tipping point*.

109       The different components of stability are all based in some way on the composition, function  
 110 and dynamics of communities. They are unlikely to be independent. Furthermore, the strength and  
 111 even the nature of relationships among stability components can change when communities are  
 112 disturbed in different ways (Donohue *et al.* 2013). This complexity has critical implications for our  
 113 understanding of the impacts of disturbances on ecosystems. It means that restricting our focus to  
 114 single measures of stability in isolation, or to amalgamated ones such as Holling’s resilience, when  
 115 they are used to reduce the multidimensional complexity of stability to a single dimension and its  
 116 measurement to a single number, risks significantly underestimating the impacts of perturbations. It  
 117 also risks incomplete understanding of the mechanisms that underpin the overall stability of  
 118 ecosystems. The multidimensionality of ecological responses demands explicit multidimensional  
 119 measurement of both disturbances and stability.

120       The definitions of the various components of stability all come with underlying assumptions  
 121   about the nature of ecosystems and the disturbances that affect them. Measures of variability, for  
 122   example, commonly assume the presence of stationary fluctuations [*i.e.* without an underlying  
 123   directional trend (Tilman *et al.* 2006; Loreau & de Mazancourt 2013)]. The ecological definitions of  
 124   resilience (Quinlan *et al.* 2016) argue for different worldviews, one where a single equilibrium  
 125   dominates, the other where two or more equilibrium domains are possible, with tipping points  
 126   between them. The Aichi Targets (UN 2010) that consider “safe ecological limits” may invoke the  
 127   latter view, as do related concepts, such as planetary boundaries, that are the subject of considerable  
 128   debate (Box 1). Other definitions may read into a simpler notion of, for example, preventing  
 129   overexploitation. Irrespective of definitions, theoretical studies of stability are generally based on  
 130   the dynamics of communities at, or very close to, some form of equilibrial state. Given the highly  
 131   dynamic nature of the natural world and the strong directionality of many elements of global  
 132   change, this limits the applicability of existing theory to the real world and creates significant  
 133   challenges for empiricists trying to test its predictions.

134

### 135   **What do ecologists measure?**

136       To understand the differences in what theoreticians and empiricists study, we surveyed three  
 137   high impact multidisciplinary journals and four leading general ecology journals: *Nature*, *Science*,  
 138   *PNAS*, *Ecology Letters*, *Ecology*, *Oikos* and *American Naturalist*. Using relevant search terms  
 139   (“ecolog\* stability”; “ecolog\* resilience”; “ecolog\* resistance”; “stability and diversity”), this  
 140   yielded 894 papers, 354 of which measured ecological stability in one or more ways. About half of  
 141   these studies were purely theoretical, the other half empirical. Of the latter, there were nearly equal  
 142   proportions of experimental and observational studies. Only 4% of papers combined both theory  
 143   and empirical measurement.

144       In our survey, 93% of theoretical studies and 85% of experimental and observational studies  
 145   focus on a single facet of stability (Fig. 2a). Some 83% of theoretical studies and 80% of



146 experimental and observational studies also focus on only a single disturbance component (Fig. 2b).  
 147 This demonstrates a restricted, largely one-dimensional, perspective. It means that we have little  
 148 understanding of either the multidimensional nature of ecological stability or the correspondence of  
 149 different components of stability to different types of perturbations.

150       There is also a significant disjoint between theoretical and empirical approaches to, and  
 151 understanding of, ecological stability. The majority (57%) of theoretical studies focus on  
 152 asymptotic stability, whereas experimental (61%) and observational (72%) studies concentrate  
 153 primarily on variability (Fig. 3a). In contrast, asymptotic stability comprises the focus of only 4%  
 154 of empirical studies, while only 18% of theoretical studies quantified variability. Only a small  
 155 minority of studies, either theoretical or empirical, examine persistence (10% of studies), resilience  
 156 (7%) or resistance (7%). Within these latter three measures, there are notable differences.  
 157 Theoretical studies most often examine persistence, resilience and a particular measure of resistance  
 158 called robustness – the susceptibility to species extinctions, usually caused by the initial loss of a  
 159 species (Solé & Montoya 2001; Staniczenko *et al.* 2010). Observational studies emphasise  
 160 resistance, while experimental studies consider resistance and resilience in equal measure. Our  
 161 survey identified very few empirical studies of robustness. Additional aspects of stability are  
 162 potentially addressed in more specialized journals than those scanned in our survey. However, the  
 163 literature we surveyed came from the general ecological journals most probably read by both  
 164 theoreticians and empiricists, potentially making the divergence we found in terms and concepts  
 165 even more significant.

166       We found similar disparities between the focus of theory and empirical research on the  
 167 different types of disturbance durations and frequencies. The majority (70%) of theoretical studies  
 168 focus on the effects of single pulse perturbations on stability (Fig. 3b). In contrast, 83% of  
 169 observational studies examine the effects of combined, multiple pulse disturbances (Fig. 1a),  
 170 usually in the form of natural environmental fluctuations. Experimental studies prioritise the effects  
 171 of press and multiple pulse disturbances in broadly equal measure (respectively, 38% and 47%).

172 Only 15% of studies we surveyed incorporate the effects of disturbance magnitude. The problem is  
 173 more acute when we account for different components of stability. For example, our survey  
 174 identified no theoretical studies of the effects of disturbance magnitude, pulse or multiple pulse  
 175 disturbance frequencies on ecological resistance. Nor did we find any experimental or observational  
 176 studies of the effects of pulse disturbances on asymptotic stability (Fig. S1). In spite of its  
 177 importance to characterising disturbances in the real world, our survey identified only one study  
 178 (van Nes & Scheffer 2004) that explored the effects of the directionality of a disturbance on  
 179 ecological stability.

180 Almost exclusively, just two characteristics of communities provide the basis upon which  
 181 studies measure ecological stability. Population or community biomass comprises the focus of  
 182 approximately two-thirds (63%) of studies included in our survey, while almost all of the remaining  
 183 studies (35%) examine the stability of taxonomic composition in some way (Fig. 3c). This pattern is  
 184 broadly consistent across both theoretical and empirical studies and across all components of  
 185 stability, except for persistence, where the majority of studies focus on composition, and  
 186 robustness, whose definition is constrained to community composition (Fig. S2). We found few  
 187 (six) studies that measured the resilience of community composition.

188 In spite of the strong policy focus on ensuring the sustained provision of ecosystem services  
 189 (*e.g.* TEEB 2010; Díaz *et al.* 2015), we found remarkably few empirical or theoretical assessments  
 190 of the stability of related ecosystem functions or processes. Only 2% of studies in our survey  
 191 examined the stability of an ecosystem function or process, in spite of their importance to the  
 192 perceived economic value of ecosystems (Armsworth & Roughgarden 2003). Of those, almost all  
 193 measured the variability of ecosystem function in time or space. We found only one study (Zavaleta  
 194 *et al.* 2010) that also examined thresholds for the persistence of multiple functions. Our survey  
 195 identified no studies of the resilience, asymptotic stability or resistance of ecosystem functions.

196 There is significant bias towards terrestrial ecosystems (52%) among empirical studies of  
 197 stability, of which most (53%) are from grasslands. Of the remaining studies, 29% are from

198 freshwater ecosystems, while only 16% are from marine systems. Experimental and observational  
199 studies are represented approximately equally across all ecosystem types.

200       What are the conclusions we draw from this? Clearly, experimentalists and empiricists can  
201 estimate the clearly-defined measures used by theoreticians. The problem is that some things are  
202 easy to measure and other things not, a distinction that likely leads to the differences we have noted.  
203 The differences are even greater on closer inspection: theory does not always address what  
204 empiricists can measure. This is, at least in part, because the mathematics of dynamical systems  
205 lacks tools for evaluating quantities of interest to empirical ecologists. Take resilience, for example.  
206 Models measuring resilience use the engagingly simple idea of asymptotic stability. They calculate  
207 return times over long intervals — when transient changes have decayed — and close to the  
208 equilibrium — where one can use linear approximations to the underlying non-linear nature of the  
209 system (Pimm 1982). Empiricists, on the other hand, tend to look at short intervals and disturbances  
210 far from the equilibrium, where transient effects in the models may be significant (De Vries *et al.*  
211 2012; Hoover *et al.* 2014; O'Connor *et al.* 2015). Here, the simplifying mathematics are  
212 unavailable, and so are ignored. The models may still provide broadly the right insights, but there is  
213 no guarantee that they do. Theoreticians could take the extra step and explore the dynamics of their  
214 models over short intervals away from equilibrium, even if only using simulations, to check their  
215 generality (*e.g.* Hastings 2004; Ives & Carpenter 2007; Ruokolainen & Fowler 2008). More  
216 generally, theoreticians might recognise that certain aspects of their theories are far more likely to  
217 be tested — and to be more widely useful — if they addressed metrics that empiricists can more  
218 easily measure (Shou *et al.* 2015).

219       A more fundamental problem arises from the lack of exploration of the multidimensional  
220 nature of either disturbances or stability. This gap in knowledge limits our ability to understand and  
221 predict the effects of disturbances on the overall stability of ecosystems. If the science of ecology is  
222 to support and inform robust and successful policy, we should close this gap.

223

## 224    **The goals of policy and their measurement**

225            Many consequences of human actions on nature are simple and have clearly defined units.  
 226    For instance, the United Nations Convention on Biological Diversity (CBD) and related  
 227    conventions sets targets that include the numbers of species and areas of habitat to be protected, and  
 228    rates of extinction, habitat loss and fragmentation, and overexploitation of fisheries and rangelands  
 229    to be minimised (UN 1992). Assisting developing countries reduce carbon emissions from  
 230    deforestation and forest degradation is the simply stated goal of the United Nations REDD  
 231    (Reducing Emissions from Deforestation and Forest Degradation in Developing Countries)  
 232    Programme (UN 2008). These may neither be easy to measure in practice nor to manage  
 233    effectively, but they do not pose conceptual challenges.

234            Much more problematic are associated terms. *Sustainability* is ubiquitous (Bosch *et al.* 2015),  
 235    and has a large associated literature. For some, it is used in a normative way, that is, as some  
 236    desired goal or set of goals. Thus, it is part of the mission of the Global Environment Facility  
 237    (GEF), and about half of the CBD's Aichi Biodiversity Targets for 2010-2020 include the word  
 238    (UN 2010). IPBES includes conservation and sustainability of ecosystem services to provide long-  
 239    term human well-being in its conceptual framework (Díaz *et al.* 2015). Responsibilities of the UK  
 240    Department for Environment, Food and Rural Affairs include sustainable development, which  
 241    China adopted explicitly as a national strategy in 1996 (Chinese Ministry of Finance *et al.* 2014).  
 242    Most commercial enterprises now include statements about corporate and environmental  
 243    sustainability in their mission statements. Normative definitions of sustainability therefore play an  
 244    important role in policy, and environmental decision makers clearly do not only concern themselves  
 245    with ecological components of stability. But neither should they ignore them.

246            We defer to the Oxford English Dictionary that defines “sustainable” as “*the quality of being*  
 247    *sustainable at a certain rate or level*” and environmentally sustainable as “*the degree to which a*  
 248    *process or enterprise is able to be maintained or continued while avoiding the long-term depletion*  
 249    *of natural resources.*” Following this, we take sustainability (in its non-normative sense) to mean

that a particular resource persists, or persists above (or below) some pre-determined level, or is resistant to disturbances. Its translation to ecological concepts is conceptually straightforward.

Other terms are less so. For example, the 20 Aichi Targets include: *safe ecological limits* (Targets 4 & 6), *degradation* (Target 5), *function* (Targets 8, 10 & 19), and *integrity* (Target 10) (UN 2010). These terms lack definitions, or have more than one definition, and have no clear units for quantification. This imprecision is unfortunate in itself (Bosch *et al.* 2015; Lu *et al.* 2015). It also denies the integration of the large body of empirical and theoretical literature that deals with broadly similar, but quantifiable, measures of multi-species systems that might provide key insights.

Differences among terms used, and in the meanings of common terms (Grimm *et al.* 1992; Grimm & Wissel 1997; Ives & Carpenter 2007; Hodgson *et al.* 2015), are likely a consequence of the different goals of theoretical and empirical ecologists and policymakers and practitioners. They also reflect the fact that ecologists have perhaps less influence on these terms and their use than we might hope. These differences create significant challenges for translating research findings into policy-relevant information, for communication among individuals from different groups, and for dealing with the complexity and multifaceted nature of ecological stability. We now examine the terms used by policymakers and practitioners, then explore the potential for common ground.

### **How do ecologists and policymakers differ in the terms they use?**

We surveyed policy targets and mission and vision statements of 42 key international agreements, organisations and agencies (Table 1) that are concerned primarily with the conservation and protection of nature. We searched for terms that are associated positively with stability. The most common terms we found were, by some distance, ‘*sustain*’ and ‘*sustainability*’. These were present in more than half of the targets and statements examined (Table 2). They occurred almost twice as frequently as the next most common terms, ‘*conserve*’ and ‘*conservation*’. We identified 14 other terms that occurred less frequently across the documents we examined (Table 2). Of all of

the terms we identified, only two, ‘*stabilise*’/‘*stable*’ and ‘*resilience*’/‘*resilient*’, have clear ecological definitions. Unfortunately, their use in the documents implied different meanings to those widely used in ecological theory, relating most strongly to, respectively, variability and resistance.

In spite of the widely different terminologies used by ecologists and policymakers and practitioners, all of the terms we identified in policy targets and statements could be associated in some way with at least one, and frequently more than one, component of ecological stability (Table 2). In fact, the stability components that associate most strongly with these terms are among the least studied by ecologists (Fig. 3a). For some terms, the link with components of stability was clear, for others less so. For example, to ‘*constrain impacts*’ necessitates increasing the resistance of systems to disturbances. It also implies increasing their resilience (*i.e.* reducing their return times). The fact that the majority of the terms used in policy integrate across different components of ecological stability means that they are also, at least implicitly, multifaceted. ‘*Sustainable*’ is a good example of this. In order to be sustainable, ecosystems must be resistant to disturbances. They must recover quickly from them (*i.e.* have high resilience). This implies that at least some properties (*e.g.* primary production) remain relatively unchanged through time (*i.e.* have high robustness, low variability) even though there may be considerable turnover in other properties (*e.g.* species composition; indeed, it may be the turnover in species composition that results in sustainable primary production).

Thus, key terms may lack unambiguous and clear definitions, and are not therefore directly quantifiable. Yet, the widespread use of such holistic terms implies that the multidimensionality of ecological stability is already integrated, even if unconsciously, in the language and targets of policymakers. This observation provides the motivation for closer integration with the science of ecology.

300

## 301 **Solutions and recommendations**

302 Nature responds to human pressures in complex ways. Conversely, political and governance  
 303 decisions often demand simplicity (OECD 2001; Harwood & Stokes 2003; Lu *et al.* 2015).  
 304 Acknowledging this dilemma is a first step towards enhancing the quality of the communication of  
 305 “stability” at the science-policy interface and within both science and policy. It is incumbent upon  
 306 ecologists to ensure that this process does not dilute the integrity of the underlying science.

307 The necessary second step involves the definition of terms and their measurement. There is a  
 308 fundamental need for interdisciplinary discussions about both of these (Box 2). Policymakers have  
 309 to attach measurable quantities to the terms used in their documents, while scientists must address  
 310 these concepts directly in their studies. The proliferation of undefined and, indeed, unmeasurable  
 311 ideals, such as many of the tasks that underpin the recently published United Nations Sustainable  
 312 Development Goals (SDGs) for the conservation of ecosystems (Goals 14 and 15), hinders progress  
 313 and is self-defeating. For example, SDG Task 14.2 sets the target that, “*By 2020, (countries will)*  
 314 *sustainably manage and protect marine and coastal ecosystems and avoid significant adverse*  
 315 *impacts, including by strengthening their resilience*”. This statement is ambiguous to the point of  
 316 being meaningless. Not a single aspect of this target is measurable. What constitutes “significant”?  
 317 What does resilience mean in this context? The goals of policy and the terminology used to describe  
 318 them *always* need to be defined and measurable.

319 Consider two examples from the Aichi Targets that contrast how measureable are their  
 320 aspirations. First, Aichi Target 11: “*By 2020, at least 17 per cent of terrestrial and inland water,*  
 321 *and 10 per cent of coastal and marine areas...are conserved through effectively and equitably*  
 322 *managed, ecologically representative and well connected systems of protected areas*”. These goals  
 323 are explicit and measureable, but those for Aichi Target 6 are not: “*By 2020 all fish and*  
 324 *invertebrate stocks and aquatic plants are managed and harvested sustainably...so that ... fisheries*  
 325 *have no significant adverse impacts on threatened species and vulnerable ecosystems and the*  
 326 *impacts of fisheries on stocks, species and ecosystems are within safe ecological limits*”. This  
 327 statement contains three particularly obscure terms that lack clear methods for measurement –

328 *sustainably*, *significant adverse impacts* and *safe ecological limits* – each of which appears to mean  
 329 two distinct things. As used in this context (see also Table 2), *sustainably* has a compositional  
 330 aspect – that species present in the system persist – and another related to biomass stability – that  
 331 variability of biomass at both population and community level is minimised at least to a level that  
 332 ensures the persistence of species. *Significant adverse impacts* requires that the persistence of both  
 333 ‘threatened species’ and the functioning of ‘vulnerable ecosystems’ is ensured, while *safe*  
 334 *ecological limits* requires ensuring the persistence of each of the biomass, composition and  
 335 functioning of ecosystems, presumably by enhancing their resistance to fishing activities.  
 336 Removing the obscure terms and replacing them with the clearly defined ones we suggest would  
 337 make the goal measureable. This would enable closer links with the supporting science and  
 338 highlight key research needs, which, in turn, make the goal attainable.

339 For their part, scientists need to take a coherent approach to quantifying stability, such as the  
 340 one we describe here. The field will not advance by publishing more, partly overlapping, definitions  
 341 of single terms used in isolation within a discipline. We need to employ broadly accepted terms and  
 342 apply them consistently across different communities. Both theoreticians and empiricists also need  
 343 to be more explicit about the basis upon which they are measuring stability. Conclusions drawn  
 344 about the factors that drive biomass resilience, for example, are likely to be very different from  
 345 those that underpin compositional resilience.

346 The third step is crucial. Both scientists and policymakers need to recognise that the  
 347 multidimensional nature of environmental change *always* requires a multidimensional assessment  
 348 of responses. To date, scientists and policymakers alike have tended to assess the response to one  
 349 driver of change using one aspect of stability or amalgamated concepts such as Holling’s resilience.  
 350 The hope is that this strategy provides a piece of the jigsaw that, in total, provides insight into the  
 351 overall complexity of responses. Rather, such simplification blurs the overall picture. For example,  
 352 increasing temporal variability of algal biomass may indicate transient dynamics in changing lake  
 353 food-webs (Carpenter *et al.* 2011). It tells us little about any underlying changes in community



354 structure that may be undermining, or indeed enhancing, resistance to different kinds of  
 355 disturbances. The one-dimensional approach to disturbances and stability means that we  
 356 underestimate the impacts of perturbations and cannot identify the mechanisms that underpin the  
 357 overall stability of ecosystem structure or functions. The existence of trade-offs (*i.e.* inverse  
 358 correlations) between different components of stability exacerbates this situation. Such trade-offs  
 359 exist in nature (Donohue *et al.* 2013) and there is some theoretical insight into why they occur  
 360 (Harrison 1979; Loreau 1994; Dai *et al.* 2015). Their existence has profound implications for  
 361 policymakers and practitioners, necessitating decisions on which aspects of stability to prioritise for  
 362 different management goals. They also provoke an environmental cost to those decisions, where  
 363 some aspects of ecological stability are necessarily diminished to enhance others. The lack of  
 364 exploration of the multidimensional nature of ecological stability means that our ability to *optimise*  
 365 the overall stability of ecosystems for different management and policy goals is at present  
 366 extremely limited.

367

368 *What science is needed to support these steps and enhance the efficacy of policy?*

369 We make three recommendations. First, the necessity for improved and mechanistic insight  
 370 into the multidimensional nature of disturbances and stability requires more realistic theory and  
 371 experimental designs and an improved ability to integrate across studies from different spatial and  
 372 temporal scales and different kinds of ecosystem (*e.g.* Peters *et al.* 2011). Even single pulse  
 373 disturbances (*e.g.*, a chemical spill) often have a legacy (*e.g.*, contamination, loss of rare species)  
 374 that corresponds to a press disturbance. Pulse and press disturbances likely affect different  
 375 components of stability in different ways. Likewise, many press disturbances exhibit clear  
 376 directionality and dynamic variation around the mean, with single extreme events occurring more  
 377 frequently. For instance, the nature of climate disruption calls for new theory (Ives *et al.* 2010;  
 378 Stenseth *et al.* 2015) and long-term experiments. These need to consider the incrementally  
 379 increasing magnitude of, for example, temperature change, and the possibility of including large

380 variability up to extreme climatic events. They must employ stability metrics that do not require  
 381 strong equilibrium assumptions (*e.g.* fixed point attractors). Moreover, they must be able to  
 382 evaluate ecosystems in continuous transient dynamics (Fukami & Nakajima 2011). The research of  
 383 theoretical and empirical ecologists has to include the complex nature of disturbances and stability,  
 384 and the result of such multidimensional approaches has to inform policymakers.

385       Some existing theoretical approaches may be extended to deal with this range of natural  
 386 complexity. For example, Floquet theory can be used to explore the stability properties of periodic  
 387 (cyclical, non-single point equilibrium) systems (*e.g.* Lloyd & Jansen 2004, Klausmeier 2008). This  
 388 can be developed in a similar way to assess how locally stable, single point equilibria respond to  
 389 perturbations. Lyapunov exponents can be used to investigate more complex, chaotic intrinsic  
 390 dynamics in naturally variable systems (Ellner & Turchin 1995). Gao *et al.* (2016) have proposed  
 391 general methods that can reduce the high dimensionality of multi-species systems to predict the loss  
 392 of resilience (defined there as the ability to avoid switching from a relatively high to much lower  
 393 mean value of a focal state variable). In parallel, new theoretical developments are starting to  
 394 explore links between what empiricists measure (*e.g.* variability) and what theoreticians analyse  
 395 (*e.g.* asymptotic resilience), showing that some fundamental relationships can be established  
 396 (Arnoldi *et al.* 2016). Together, these approaches offer promising new directions for further  
 397 theoretical research that incorporate the sort of complexities empiricists commonly encounter in  
 398 their study systems.

399       Second, we need simple, yet scientifically sound, ways to integrate across the multiple  
 400 dimensions to quantify the overall stability of ecosystems. These methods will need to distil the  
 401 most important elements of stability and make accurate quantitative measures on each dimension.  
 402 Only then can we combine them (Fig. 4). These methods also need to be adaptable to the priorities  
 403 of specific policies. Such adaptation is fundamental to optimising the overall stability of ecosystem  
 404 structure and/or functioning for different management and policy objectives. Agricultural  
 405 management, for example, aims to minimise variability of yield production and maximise

406 resistance of biomass to pathogens and insect pests. In contrast, many conservation programs might  
 407 try to maximise the compositional persistence and resilience of communities (rare species are often  
 408 the most endangered and they tend to determine the slowest return times of the system). Such semi-  
 409 quantitative methods of holistic assessment may seem too broad-brush and inaccurate to satisfy  
 410 many scientists. They may also be too complex for some policymakers. The solution has to be  
 411 something that sits between the two.

412 Third, we need to evaluate and monitor stability through space and time. Ecologists have  
 413 experience in doing this for single populations and key functional groups (*e.g.* Ives *et al.* 2008;  
 414 Carpenter *et al.* 2011) and, more recently, for monitoring changes in the provision of ecosystem  
 415 goods and services (Tallis *et al.* 2012). Monitoring the dynamic stability of whole networks has  
 416 largely been the province of economists, among others, with numerous financial stability  
 417 monitoring programs continuously tracking sources of systemic risk (Adrian *et al.* 2014).  
 418 Analogous programs for monitoring the dynamic multidimensional stability of whole ecological  
 419 systems over time and space are essential to help assess the effectiveness of policy and management  
 420 actions. These programmes are needed to help identify ecosystems whose stability is being  
 421 compromised in the face of global change.

422

## 423 **Conclusions**

424 There are policies concerned with the protection of nature that set defined and measurable  
 425 targets. Aichi Target 5 (UN 2010) constitutes a good exemplar: “*By 2020, the rate of loss of all*  
 426 *natural habitats, including forests, is (to be) at least halved and where feasible brought close to*  
 427 *zero*”. This statement is clear and unambiguous – progress can be quantified, success or failure  
 428 evaluated. It exemplifies the only way that policies can effect meaningful change.

429 Such policies are in the minority. Many policy documents describe targets that may appear,  
 430 on face value, explicit and measurable, yet contain terms that are ambiguous, or have multiple  
 431 definitions that mean different things to different people. Such targets cannot be connected to

432 measureable ecological processes or properties. Policies aiming to increase “resilience” provide  
 433 pervasive examples. In fact, the majority of policy documents we surveyed contain goals using  
 434 terms that lack definition within ecology. Such ambiguity paralyses policy.

435       This incoherence is, at least in part, a consequence of the inconsistent and one-dimensional  
 436 approach that ecologists have taken to ecological stability. This approach has led to confused  
 437 communication of the nature of stability and the level of our insight into it. Disturbances and  
 438 stability are multidimensional. Our understanding of them is not. We have a remarkably poor  
 439 understanding of the impacts on stability of the characteristics that define many, perhaps all, of the  
 440 most important elements of global change.

441       The solution requires a range of actions. We need more realistic theory based on measures  
 442 that are of practical significance and empirically quantifiable. Empiricists need to test this theory at  
 443 a range of spatial and temporal scales. Policymakers need to use these defined and measurable  
 444 quantities in their targets. Most importantly, theoreticians, empiricists, policymakers and  
 445 practitioners each need to incorporate the multidimensional complexity of natural responses to  
 446 environmental change into their research, policies and actions.

447

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460

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747 **Table 1.** International agreements, organisations and agencies whose policy targets and mission and vision statements we searched for terms associated  
 748 with ecological stability.

Entity	Stability related term(s) found	Document link
Aichi biodiversity targets (CBD)	'integrity'; 'safe ecological limits'; 'resilience'; 'sustain'; 'conserve'	<a href="http://www.cbd.int/sp/targets/">http://www.cbd.int/sp/targets/</a>
Biodiversity International	'sustain'; 'safeguard'	<a href="http://www.biodiversityinternational.org/about-us/who-we-are/">http://www.biodiversityinternational.org/about-us/who-we-are/</a>
Birdlife International	'sustain'; 'maintain'	<a href="http://www.birdlife.org/worldwide/partnership/our-vision-mission-and-commitment">http://www.birdlife.org/worldwide/partnership/our-vision-mission-and-commitment</a>
Convention on Biological Diversity	'sustain'; 'conserve'	<a href="http://www.cbd.int/convention/articles/default.shtml?a=cbd-01">http://www.cbd.int/convention/articles/default.shtml?a=cbd-01</a>
Conservation International	'healthy'; 'sustainable'; 'stable'	<a href="http://www.conservation.org/about/Pages/default.aspx#mission">http://www.conservation.org/about/Pages/default.aspx#mission</a>
UK Department for Environment, Food & Rural Affairs	'safeguard'	<a href="https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs/about">https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs/about</a>
Diversitas (now rolled into Future Earth)	'secure'; 'conserve'; 'sustain'	<a href="http://www.diversitas-international.org/about/mission-and-history">http://www.diversitas-international.org/about/mission-and-history</a>
Earthwatch	'sustain'	<a href="http://eu.earthwatch.org/about/earthwatch-mission-and-values">http://eu.earthwatch.org/about/earthwatch-mission-and-values</a>
European Environment Agency	'sustainable'	<a href="http://www.eea.europa.eu/about-us">http://www.eea.europa.eu/about-us</a>
European Platform for Biodiversity Research Strategy	'maintain'; 'sustain'; 'conserve'	<a href="http://www.epbrs.org">http://www.epbrs.org</a>
Earth System Science Partnership	'sustainable'	<a href="http://www.essp.org">http://www.essp.org</a>
European Union Biodiversity Observation Network	None found	<a href="http://www.eubon.eu/show/project_2731/">http://www.eubon.eu/show/project_2731/</a>
Food and Agriculture Organisation	'security'; 'sustainable'	<a href="http://www.fao.org/about/en/">http://www.fao.org/about/en/</a>
Future Earth	'sustainable'	<a href="http://www.futureearth.org">http://www.futureearth.org</a>
Global Environment Facility	'sustainable'	<a href="https://www.thegef.org/gef/whatisgef">https://www.thegef.org/gef/whatisgef</a>
GreenPeace	'protect'	<a href="http://www.greenpeace.org/international/en/about/our-core-values/">http://www.greenpeace.org/international/en/about/our-core-values/</a>
International Association for Landscape Ecology	'altered'	<a href="http://www.landscape-ecology.org/index.php?id=14">http://www.landscape-ecology.org/index.php?id=14</a>
Intergovernmental platform on biodiversity and ecosystem services	'conserve'; sustain'	<a href="http://dx.doi.org/10.1016/j.cosust.2014.11.002">http://dx.doi.org/10.1016/j.cosust.2014.11.002</a>
Intergovernmental Panel on Climate Change	None found	<a href="http://www.ipcc.ch/organization/organization.shtml">http://www.ipcc.ch/organization/organization.shtml</a>
International tropical timber organisation	'sustainable'; 'conservation'	<a href="http://www.itto.int/about_itto/">http://www.itto.int/about_itto/</a>
International Union for Conservation of Nature	'conserve'; 'sustain'	<a href="http://www.iucn.org">http://www.iucn.org</a>
LifeWatch infrastructure for biodiversity and ecosystem research	None found	<a href="http://www.lifewatch.eu">http://www.lifewatch.eu</a>

Living with Environmental Change	None found	<a href="http://www.lwec.org.uk/about">http://www.lwec.org.uk/about</a>
Natural Capital Project	'sustainable'	<a href="http://www.naturalcapitalproject.org">http://www.naturalcapitalproject.org</a>
Organisation for Economic Co-operation and Development	'sustainable'; 'resilience'	<a href="http://www.oecd.org/env/">http://www.oecd.org/env/</a>
Rainforest Alliance	'conserve'; 'sustain'; 'safeguard'	<a href="http://www.rainforest-alliance.org/about">http://www.rainforest-alliance.org/about</a>
The Economics of Ecosystems and Biodiversity	None found	<a href="http://www.teebweb.org/about/">http://www.teebweb.org/about/</a>
The Nature Conservancy	'conserve'	<a href="http://www.nature.org/about-us/vision-mission/index.htm?intc=nature.tnav.about.list">http://www.nature.org/about-us/vision-mission/index.htm?intc=nature.tnav.about.list</a>
United Nations Reducing Emissions from Deforestation and Forest Degradation	'constrain impacts'	<a href="http://www.un-redd.org">http://www.un-redd.org</a>
United Nations Convention to Combat Desertification	'sustain'; 'secure'	<a href="http://www.unccd.int/en/Pages/default.aspx">http://www.unccd.int/en/Pages/default.aspx</a>
United Nations Environment Programme	'sustain'	<a href="http://www.unep.org/Documents.Multilingual/Default.asp?DocumentID=43">http://www.unep.org/Documents.Multilingual/Default.asp?DocumentID=43</a>
Kyoto protocol (UNFCCC)	'stabilise'	<a href="http://unfccc.int/kyoto_protocol/items/2830.php">http://unfccc.int/kyoto_protocol/items/2830.php</a>
United Nations Sustainable Development Goals	'security'; 'sustainable'; 'resilient'; 'conserve'; 'protect'	<a href="https://sustainabledevelopment.un.org/post2015/transformingourworld">https://sustainabledevelopment.un.org/post2015/transformingourworld</a>
Wetlands International	'resilience'	<a href="http://www.wetlands.org/Aboutus/VisionMission/tabid/58/Default.aspx">http://www.wetlands.org/Aboutus/VisionMission/tabid/58/Default.aspx</a>
World Meteorological Organisation	'safety'	<a href="https://www.wmo.int/pages/about/mission_en.html">https://www.wmo.int/pages/about/mission_en.html</a>
World Nature Organisation	'sustainable'	<a href="http://www.wno.org/mission">http://www.wno.org/mission</a>
Stern Review on the Economics of Climate Change	None found	<a href="http://mudancasclimaticas.cptec.inpe.br/~rmclima/pdfs/destaques/sternreview_report_complete.pdf">http://mudancasclimaticas.cptec.inpe.br/~rmclima/pdfs/destaques/sternreview_report_complete.pdf</a>
Worldwatch Institute	'sustainable'	<a href="http://www.worldwatch.org/mission">http://www.worldwatch.org/mission</a>
World Wildlife Fund for Nature	'harmony'; 'safeguard'	<a href="http://wwf.panda.org/wwf_quick_facts.cfm">http://wwf.panda.org/wwf_quick_facts.cfm</a>
York Environment Sustainability Institute	'resilient'; 'maintain'; 'conservation'	<a href="http://www.york.ac.uk/media/yesi/downloaddocuments/YESI%20Brochure-WEB.pdf">http://www.york.ac.uk/media/yesi/downloaddocuments/YESI%20Brochure-WEB.pdf</a>
Convention on International Trade in Endangered Species of Wild Fauna and Flora	'survival'	<a href="http://www.cites.org/eng/disc/what.php">http://www.cites.org/eng/disc/what.php</a>
International Whaling Commission	'conservation'	<a href="https://iwc.int/history-and-purpose">https://iwc.int/history-and-purpose</a>

750 **Table 2.** Stability-like terms used in policy targets and mission and vision statements of the international agreements, organisations and agencies  
 751 highlighted in Table 1, ranked in order of frequency of occurrence, and the components of stability that they associate with in the context of their use.  
 752 The use of resistance here incorporates robustness. We assume that the necessity for systems to be asymptotically stable around an equilibrium point or  
 753 limit cycle is implicit in the use of every term.

754

Terms used in policy	Occurrence	Stability component(s) associated most strongly	Other associated stability components
‘sustain’/‘sustainable’	25/42	Persistence	Resistance, Resilience, Variability
‘conserve’/‘conservation’	13/42	Persistence	Resistance, Resilience
‘resilience’/‘resilient’	5/42	Resistance	Resilience, Persistence
‘safeguard’	4/42	Persistence	Resistance
‘maintain’	3/42	Persistence	Resistance, Variability
‘secure’/‘security’	4/42	Persistence	Resistance, Resilience
‘stabilise’/‘stable’	2/42	Variability	Resistance, Resilience, Persistence
‘protect’	2/42	Persistence	Resistance
‘altered’	1/42	Persistence	Resistance
‘constrain impacts’	1/42	Resistance	Resilience
‘harmony’	1/42	Variability	
‘healthy’	1/42	Resistance	Resilience
‘integrity’	1/42	Resistance	Persistence, Resilience
‘safety’	1/42	Resistance	Persistence
‘survival’	1/42	Persistence	Resistance, Resilience
‘safe ecological limits’	1/42	Resistance	Persistence, Resilience, Variability, Multiple locally stable equilibria

755

## 756 **Figure legends**

757

758 **Fig. 1.** Conceptual summary of multifaceted disturbances. Characterisation of pure pulse  
 759 and press disturbances (a) that are the focus of most theoretical and experimental studies,  
 760 and an intermediate multiple pulse form of disturbance (dotted blue line) that is also  
 761 studied frequently, mostly in the form of natural environmental fluctuations in  
 762 observational studies. Most disturbances are, however, neither pulse nor press and  
 763 instead change in magnitude over time (b), frequently with shifting mean and variance  
 764 components. We lack theory and have very limited empirical evidence on the impacts of  
 765 these directional aspects of disturbances on ecological stability, yet they represent many  
 766 of the most important and widespread aspects of human impacts (c).

767

768 **Fig. 2.** The restricted focus of studies on single components of stability (a) and disturbances  
 769 (b). The total number of studies is slightly lower in (b) because some of the studies we  
 770 surveyed did not incorporate an explicit disturbance.

771

772 **Fig. 3.** Overview of studies of ecological stability. Number of studies identified by our  
 773 survey of the literature that quantified different facets of stability (a), examined the effects  
 774 of different components of disturbance on those (b), and that used biomass, taxonomic  
 775 composition or ecosystem functioning as a basis for measuring stability (c).

776

777 **Fig. 4.** Integrating across multiple dimensions to quantify overall ecological stability. We  
 778 suggest a method that incorporates multiple stability facets and allows for their differential  
 779 weighting. This method is based loosely on one developed for the assessment of biodiversity  
 780 effects on multiple ecosystem functions (Byrnes *et al.* 2014). A multiple-criteria decision-  
 781 making approach would also be suitable here. First, the method identifies which stability

782 facets can be quantified and provides a scoring system for each facet (a). This could be as  
783 simple as low, moderate and high, although more sophisticated scoring systems could be  
784 developed. It then applies a weighting factor to each score, depending on their perceived  
785 relative importance for a given policy or management practice (b). The sum of the weighted  
786 scores then corresponds to the stakeholder's value of the stability of the system (c). Even  
787 though different facets of stability may be correlated, there is no need to assume this. Trade-  
788 offs and synergies among stability metrics can be incorporated, but the method does not  
789 assume dependencies.

## 790 **Box 1: Why the attempt to define planetary boundaries is flawed**

791 Human actions are changing the biosphere in unprecedented ways. One view is that, given the  
792 magnitude and novelty of these impacts, there will be thresholds, beyond which abrupt non-linear  
793 change will bring the biosphere to a new and undesirable equilibrium. This view of nature, founded  
794 upon Holling's (1973) definition of resilience, explicitly engages policymakers with its invocation  
795 of catastrophic tipping points and the conclusion that Earth has already exceeded them. The view is  
796 becoming increasingly pervasive in the scientific literature.

797 Certainly, there may be systems that show the tipping points that underpin this worldview.  
798 Importantly, there is nothing to suggest they are ubiquitous and so demand their having logical  
799 primacy. Nature might work this way sometimes, but there is no compelling argument that it must.

800 In attempting to define global tipping points and, from those, "planetary boundaries",  
801 Rockström *et al.* (2009) have extended this view to circumstances where it is unlikely to operate.  
802 We take as an example the variable they deemed already to be outside the planetary boundary  
803 arising from our work (Pimm *et al.* 1995; Pimm *et al.* 2014): the rate of species extinctions. The  
804 metric is simple — a fraction of species going extinct per unit time. The comparison to a natural  
805 background rate is also conceptually easy, though there are practical difficulties (De Vos *et al.*  
806 2015). The notion that the current global species extinction rate — about a thousand times higher  
807 than background — has exceeded some tipping point where catastrophic ecological changes must  
808 follow is problematical in several ways (Mace *et al.* 2014).

809 First, it is not clear over what spatial and temporal scales extinction rates have exceeded the  
810 boundary. For example, how are the locally high rates of plant and animal extinctions on remote  
811 Pacific Islands following first contact with Polynesians and later with Europeans supposed to "tip"  
812 processes globally or (say) in the Amazon? And over what time period might these catastrophic  
813 changes unfold?

814 Subsequent clarifications by Rockström and colleagues (Stockholm Resilience Centre 2012;  
815 Steffen *et al.* 2015) indicate that the proposed 'planetary' boundary for extinctions operates at

816 regional scales, but they are not explicit in defining either the spatial or temporal extents of these  
817 regions. This leaves open the vitally important question for policymakers of what scales are most  
818 important.

819       Second, there are models of the consequences of losing species and how many more species  
820 will be lost consequently at local and regional scales (Pimm 1991). None shows the kind of  
821 runaway processes that Rockström and colleagues imagine. Certainly, there is both an extensive  
822 theoretical and empirical literature on how species richness (as opposed to its rate of change) affects  
823 a variety of ecosystem functions including primary productivity and nutrient cycling (Loreau *et al.*  
824 2001; Cardinale *et al.* 2012). This literature shows degradation as species numbers decline  
825 (Cardinale *et al.* 2011), but no clear thresholds.

## 826 **Box 2: Learning from experience: biodiversity-ecosystem functioning and service provision**

827 Even when theoreticians and empiricists converge in what they quantify, there is no guarantee  
828 of immediate and successful translation into the policy and management arena. Research on  
829 Biodiversity-Ecosystem Functioning (BEF) and Biodiversity-Ecosystem Services (BES)  
830 relationships exemplifies this and, as such, we can learn from it.

831 A large body of experiments (> 600 since 1990) developed in close relation with  
832 mathematical theory and showed how genetic, species and functional diversity of organisms  
833 regulate basic ecological processes – functions – in ecosystems (Cardinale *et al.* 2012). As a result,  
834 there is now unequivocal evidence supported by theory that biodiversity loss reduces biomass  
835 production, decomposition and recycling of essential nutrients, and the efficiency at which  
836 ecosystems capture biological resources. In parallel, a strong policy impulse developed trying to  
837 guarantee the provision of ecosystem services to society, now under the umbrella of the recently  
838 established Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services  
839 (IPBES; Díaz *et al.* 2015). Despite the mechanistic understanding of the effects of biodiversity on  
840 functioning provided by theoreticians and empiricists, the mechanistic links between biodiversity  
841 and ecosystem services are far from being established. This disconnect effectively impairs the  
842 distillation of conclusions to inform policy on how biodiversity loss will affect service provisioning  
843 and regulation and, ultimately, human wellbeing.

844 An example is Payment for Ecosystem Services (PES), where beneficiaries of nature's  
845 services pay owners or stewards of ecosystems that generate those services. Naeem *et al.* (2015)  
846 suggested recently that few PES studies get the science right, with most projects based on weak  
847 scientific foundations. The main reason for this was poor interdisciplinary communication and  
848 coordination. The absence of unifying definitions and associated metrics, baseline data, monitoring,  
849 recognition of the dynamic nature of ecosystems, and poor interdisciplinary communication and  
850 coordination helps to explain this gap. The BEF community measures functions without linking  
851 those to known services. The BES community commonly describe services without linking them to



852 their underlying ecological function. A more active communication and convergence on what to  
853 measure and at what scale, and how to monitor over space and time is needed (Cardinale *et al.*  
854 2012; Naeem *et al.* 2015).